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Age-Specific Offspring Mortality Economically Tracks Food Abundance in a Piscivorous Seabird

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ABSTRACT: Earlier offspring mortality before independence saves resources for kin, which should be more beneficial when food is short. Using 24 years of data on age-specific common tern (*Sterna hirundo*) chick mortality, best described by the Gompertz function, and estimates of energy consumption per age of mortality, we investigated how energy wasted on nonfledged chicks depends on brood size, hatching order, and annual abundance of herring (*Clupea harengus*), the main food source. We found mortality directly after hatching (Gompertz baseline mortality) to be high and to increase with decreasing herring abundance. Mortality declined with age at a rate relatively insensitive to herring abundance. The sensitivity of baseline mortality to herring abundance reduced energy wasted on nonfledged chicks when herring was in short supply. Among chicks that did not fledge, last-hatched chicks were less costly than earlier-hatched chicks because of their earlier mortality. However, per hatchling produced, the least energy was wasted on chicks without siblings because their baseline mortality was most sensitive to herring abundance. We suggest that earlier mortality of offspring when food is short facilitates economic adjustment of posthatching parental investment to food abundance but that such economic brood reduction may be constrained by sibling competition.

Keywords: aging, brood reduction, brood survival, maternal effects, parent-offspring conflict, sibling competition.

Introduction

Mortality typically peaks at the start of life (Levitis 2011; Colchero et al. 2016), but age-specific mortality before independence—in contrast to age-specific mortality of adults—has received little scientific attention within an evolutionary framework. This may stem from the fact that any mortality before the onset of reproduction will nullify an individual's reproductive value regardless of the exact age of its mortality. Yet more than 5 decades ago, Hamilton (1966) noted that early individual mortality may enhance the survival of a close relative that competes over the same resources, causing the strength of selection against preindependence mortality to increase with age (also see Lee 2003, 2008). Mechanistically, Hamilton was mostly concerned with age-specific selection against the expression of genetic disorders, but a mechanism in which selection for early mortality would depend on the environment was envisaged nearly 2 decades earlier (Lack 1947). Specifically, Lack (1947) suggested that asynchronous hatching in birds causes asymmetry in the competitive ability of offspring, resulting in an early mortality of the late-hatching offspring when food is short. Despite the obvious disadvantage for the individuals that hatched late, their early mortality may lead to higher fitness returns for the parents than an even allocation of food among offspring when food availability is reduced. Such fitness benefits would enable hatching asynchrony and the corresponding early mortality to evolve.

The parental strategy of creating hatching asynchrony is typically supported with additional prenatal maternal effects—such as a decreasing allocation of resources to eggs (Slagsvold et al. 1984) or differential hormone allocation (Muller and Groothuis 2013) over the laying order—and is referred to as a brood reduction strategy (Ricklefs 1965). Initial overproduction of offspring combined with the early termination of parental care for excess offspring with a brood reduction strategy is not limited to birds and is predicted to evolve when food abundance is variable and difficult to predict at the time of offspring conception (Temme and Charnov 1987; Kozlowski and Stearns 1989). Field studies have indeed shown that maternal effects that promote initial disparities among siblings may be effective in reducing brood size when food is short (Gibbons 1987; Magrath 1989; Wiebe and Bortolotti 1995; Royle and Hamer 1998; Sasvari et al. 1999; Forbes and Wiebe 2010), but more detailed knowledge on how food availability affects age-specific mortality patterns of offspring with differential starting positions in a competitive environment appears to be lacking.

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Here we analyze 24 years of data on prefledging age-specific survival of common tern (*Sterna hirundo*) chicks. Common terns are piscivorous seabirds that heavily rely on the abundance of small pelagic fish, most importantly Atlantic herring (*Clupea harengus*), to feed their chicks (Dänhardt and Becker 2011). They lay small clutches of one to three eggs, with egg size decreasing and eggs hatching asynchronously in the order of laying (Nisbet and Cohen 1975; Bollinger 1994; Garcia et al. 2011). Survival of hatchlings to fledging is highly variable and heavily dependent on hatching order (Langham 1972; Bollinger 1994; Vedder et al. 2017) and food abundance (Dänhardt and Becker 2011). We have previously shown that the age-specific chick mortality hazard is best described by a Gompertz function (Vedder et al. 2017). The Gompertz hazard function is defined by parameters a, b, and time t:

$$h(t, a, b) = ae^{bt},$$

where a represents the baseline (or initial) mortality hazard (i.e., h at $t = 0$) and b the exponential rate of change in mortality hazard with age t (Ricklefs and Scheuerlein 2002; Kirkwood 2015). Differences in fledging success may thus arise from effects on baseline mortality (a) and/or effects on how fast mortality changes with age (b). Although the same fledging success can result from different combinations of a and b, these combinations may have different consequences for the amount of energy the nonsurviving chicks have consumed before their death (Vedder et al. 2017).

A specific combination of Gompertz parameters a and b will provide an estimate for fledging success (survival to fledging age in the Gompertz survival function) and the distribution of ages of mortality (the Gompertz probability density function), with the latter allowing an estimate of the amount of energy wasted on chicks that did not fledge per chick that hatches (see "Material and Methods"). This measure can be considered a proxy of the energetic cost that goes to producing a chick under a given level of food availability that does not result in the benefit of producing a fledgling—the energy wasted per chick that hatches. If decreased fledging success with lower food availability does not change the relative distribution of ages of mortality before fledging, the energy wasted on unsuccessful offspring will increase as food becomes scarcer at a rate that is inversely proportional to the decrease in fledging success. However, if low food availability would shift the relative distribution of ages of chick mortality to earlier mortality, the energy wasted per chick that hatches would be less dependent on food availability than fledging success would be. As such, under a brood reduction strategy we may expect a decline in fledging success with reduced food abundance to be achieved without a concomitant increase in energy wasted per chick that hatches. Using estimates of energy consumption of common tern chicks for every age of mortality before fledging (from Vedder et al. 2017), we here explore in detail how brood size, hatching order, and annual food abundance interact to determine age-specific offspring mortality, fledging success, and energy wasted on nonfledged offspring in a population of free-living birds.

Material and Methods

Study Population and Data Collection

Data were collected in a breeding colony of common terns, located at the Banter See in Wilhelmshaven at the German North Sea coast (53°36′N, 08°06′E). In common terns, both parents incubate and feed the chicks, extrapair paternity is rare, and offspring sex does not vary with hatching order (Gonzalez-Solis et al. 2001; Becker and Ludwigs 2004; Benito et al. 2013), nor does fledging success differ between the sexes (Vedder et al. 2016). The Banter See colony site consists of six rectangular concrete islands, each measuring 10.7 m × 4.6 m. The islands are surrounded by 60-cm-high walls that protect against flooding and prevent chicks from leaving the islands before fledging. Each year since 1992, all nests were systematically checked at least three times a week throughout the breeding season (May–August). All newly hatched chicks were ringed and their ages were estimated in days (between 0 and 2 days old) on the basis of a combination of size, developmental stage, dryness of down feathers, and retraction of the yolk sac. In a minority of cases where two chicks of the same brood were estimated to be of the same age, they were still assigned a separate hatching order on the basis of the above criteria. Brood size was defined as the number of chicks that hatched per clutch. In broods of two, the second-hatched chick hatched on average 1.08 ± 0.02 days (±SE) later than the first-hatched chick. In broods of three, the second- and third-hatched chicks hatched on average 0.68 ± 0.02 and 1.99 ± 0.02 days later than the first-hatched chick. At all checks, the status of individual chicks was recorded as alive, missing, or dead. Missing chicks younger than the minimal fledging age (24 days) were assumed to have died from intraspecific aggression, as cases of small chicks getting thrown in the water by adult conspecifics are regularly witnessed, while predation is not. This intraspecific aggression may result from parents trying to avoid adoption of unrelated chicks by being aggressive toward young chicks that are not in their nest as well as from adults stealing fish from young chicks, with some young chicks remaining attached to the fish and dropping off only when the adult is midair. Our data set included all chicks that hatched in the colony between 1992 and 2015 (n = 15,823 chicks from 6,998 broods, average per year = 659 chicks and 292 broods).

As a measure of annual food abundance, we used the ICES North Sea herring recruitment index (ICES 2016), which was previously shown to best predict fledging suc-

cess in the colony (Dänhardt and Becker 2011). The recruitment index for North Sea herring is the total abundance of juvenile herring 0-ringers (individuals hatched in the previous winter) in the survey area, measured with a fine-meshed pelagic trawl net, the so-called midwater ring net (or MIK-trawl). The MIK-trawl is part of the International Bottom Trawl Survey in the first quarter, meaning that the data for index calculation are collected between January and March. The index represents North Sea wide numbers of recruits (in thousands). In our analyses, we standardized the index (average = 0, SD = 1) to allow an easier interpretation of the effect on herring abundance on age-specific mortality.

Across all 24 years, annual variation in population average number of fledglings per brood was strongly positively related to the North Sea herring index ($r^2 = 0.359$; fig. S1*A*; figs. S1–S3 are available online). This was mainly caused by variation in chick mortality, because average annual clutch and brood sizes were less strongly related to the herring index ($r^2 = 0.078$ and $r^2 = 0.148$; fig. S1*A*). Indeed, the index explained 37% of the variation in annual fledging success of hatchlings (fig. S1*B*). Hatching asynchrony was only weakly related to the herring index, with only the interval between the first and third hatchling slightly decreasing in years with high herring abundance ($r^2 = 0.095$; fig. S2). The juvenile herring that the common terns utilize to feed their chicks have not yet arrived in their coastal nurseries during clutch formation and will reach their nurseries and the common tern breeding area only during chick rearing. Hence, although the ICES North Sea herring recruitment index predicts common tern fledging success, the terns can poorly use it as a cue to adjust their clutch size, explaining why effects of food abundance primarily occur after hatching.

Survival Analyses

The time to mortality for each hatchling was defined as the number of days between hatching and its observed death or missing status. Since the earliest fledglings fledge 24 days after hatching, chicks that survived to 24 days were considered as fledged and analyzed as right-censored cases; that is, the death event was not observed during the checks. Of all chicks that hatched, 54.1% died during the first 24 days.

Because survival to fledging varies considerably between years (O. Vedder, I. Pen, and S. Bouwhuis, unpublished manuscript), we first confirmed that the Gompertz function performs well in describing the age specificity of chick mortality at the annual level. To this end, we plotted annual Gompertz survival functions derived from a model that allowed both baseline mortality (Gompertz *a*) and the rate of change with age (Gompertz *b*) to vary between years. This model provided a better fit than models without annual variation in *a*, *b*, or both (table S1; tables S1, S2 are available online) and generally fitted the annual raw data well (fig. S3).

To estimate effects of brood size and hatching order, we used a six-level categorical variable that represents all possible combinations of brood size (BS) and hatching order (HO): BS = 1; BS = 2, HO = 1; BS = 2, HO = 2; BS = 3, HO = 1; BS = 3, HO = 2; and BS = 3, HO = 3 (for sample sizes per category, see table S2). This categorical variable was previously estimated as providing the best fit for the probability to survive until fledging, effectively indicating a statistically significant interaction effect between brood size and hatching order on survival (O. Vedder, I. Pen, and S. Bouwhuis, unpublished manuscript). Because we have previously shown that chicks of the six BS-HO categories express differences in baseline mortality and in the rate of change in mortality with age (Vedder et al. 2017), we here tested whether adding effects of annual herring abundance on baseline mortality and/or rate of change in mortality with age improved model fit. In addition, we tested whether interactive effects between the six BS-HO categories and annual herring abundance on baseline mortality and/or rate of change in mortality with age further improved model fit. Models were ranked according to their Akaike information criterion value and run using the procedure flexsurvreg in the package flexsurv (Jackson 2016) in R version 3.2.4 (R Development Core Team 2016). Standard errors in figure 1 were estimated by nonparametric bootstrapping with 1,000 replicates, with the R package boot (Canty and Ripley 2017). The raw data are deposited in the Dryad Digital Repository (https://doi.org/10.5061/dryad.ck1rb1g; Vedder et al. 2019).

Energy Consumption of Nonfledged Offspring

To estimate the amount of metabolizable energy wasted by nonfledged chicks, we used the estimates of total metabolizable energy intake (TME; kJ) between hatching and mortality for chicks that died at each age of prefledging mortality (days) presented by Vedder et al. (2017). These estimates are based on age of mortality–specific mass growth curves (Vedder et al. 2017) and mass-specific metabolism estimates, obtained with the doubly labeled water method in common tern chicks (Klaassen 1994). The age of mortality–specific TME estimates were multiplied with the probability for a hatchling to die at that age, as calculated from the Gompertz probability density function:

$$p(t, a, b) = ae^{bt}e^{-(a/b)(e^{bt}-1)}.$$

The sum of these values for age of mortality 0–23 was subsequently used as an estimate of the amount of metabolizable energy wasted on nonfledged chicks (kJ) per hatched chick, under the given values of Gompertz *a* and *b*. To estimate the metabolizable energy wasted per nonfledged chick,

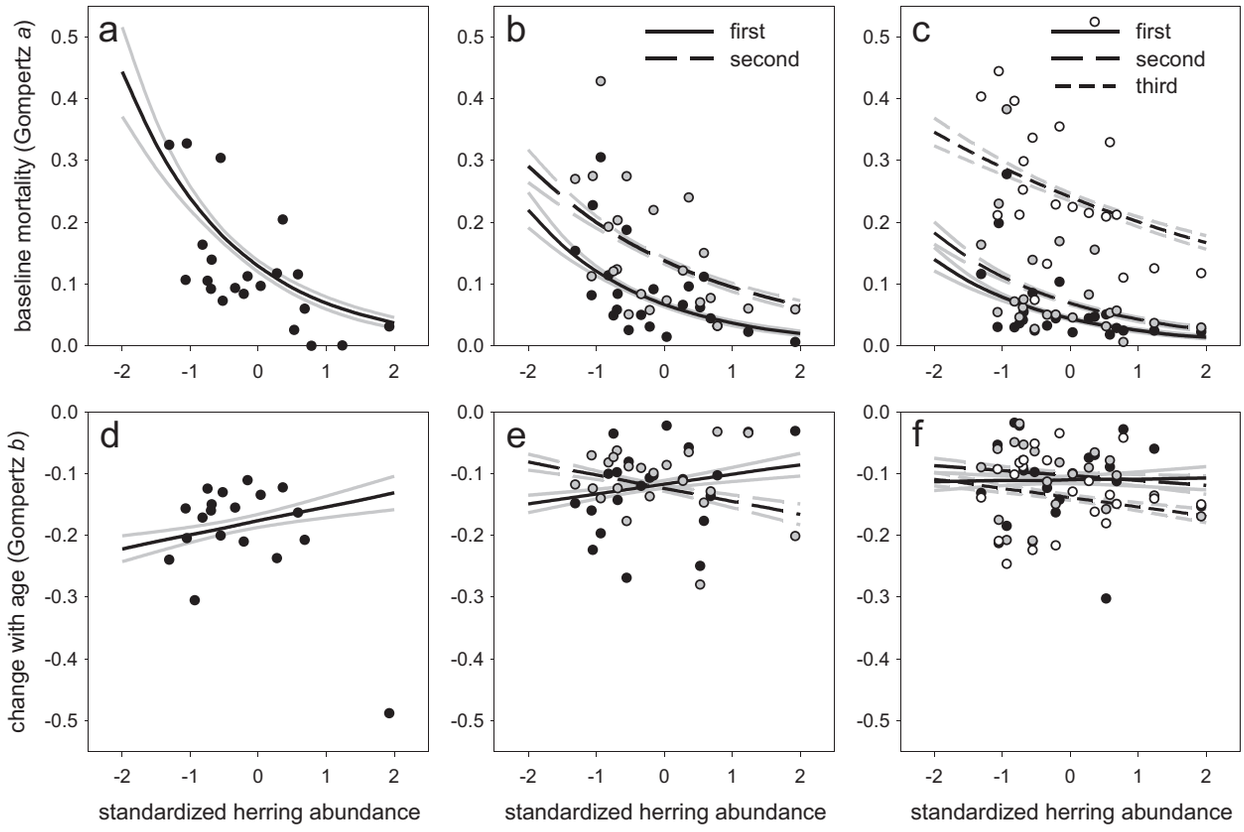


Figure 1: Estimated Gompertz parameters of common tern chick survival in relation to standardized North Sea herring abundance per brood size and hatching order. *a–c*, Baseline mortality estimates (Gompertz *a*) for brood sizes 1–3. *d–f*, Rate of change in mortality with age estimates (Gompertz *b*) for brood sizes 1–3. Data points represent parameters estimated per year, brood size, and hatching order (black = first; gray = second; white = third) separately, but the lines (black = averages; gray = ±1 SE) were fitted on the basis of the complete data set of ages of mortality while allowing them to vary with herring abundance, brood size, and hatching order.

the estimate per hatched chick was divided by the probability that a chick did not fledge. We used the values of Gompertz *a* and *b* that were estimated by the best-fitting survival model for the six different combinations of brood size and hatching order and a range of annual herring abundances (from −2 to 2 SD) to evaluate how the amount of wasted TME varies with brood size, hatching order, and herring abundance.

Results

Mortality Hazard with Age

A model that allowed both the baseline mortality and the rate of change in mortality hazard with age of chicks of different brood size and hatching order to vary with annual herring abundance provided the best fit to the data (table 1). Chicks of all brood sizes and hatching orders had their baseline mortality hazard (Gompertz *a*) decline with herring abundance, but baseline mortality of single chicks (brood size = 1) was highest at low herring abundance and declined stronger with increasing herring abundance compared with that of chicks with siblings (fig. 1*a*–1*c*). Although baseline mortality hazards were considerably higher for the later-hatching chicks within a brood, their baseline mortality declined with increasing herring abundance in a way similar to that of first-hatched chicks (fig. 1*b*, 1*c*).

Mortality declined with age for chicks of all brood sizes and hatching orders (i.e., Gompertz *b* was always negative), but the rate of exponential decline in mortality with age appeared to be less consistently affected by herring abundance than the baseline mortality (fig. 1). The mortality hazard of single chicks and chicks that hatched first in their brood declined less steeply with age when herring was abundant compared with when herring was rare (fig. 1*d*–1*f*). This may be due to low baseline mortality allowing less scope for improvement in survival with age when herring was abundant. Indeed, later-hatching chicks—which never reached the low levels of baseline mortality of single and first-hatched chicks with high herring abundance—experienced a somewhat stronger decline in mortality hazard with age when herring

Table 1: Akaike information criterion (AIC) values of Gompertz survival models testing for effects of North Sea herring abundance, brood size (BS) and hatching order (HO) on baseline mortality, and rate of change in mortality with age of common tern chicks, ranked from best to worst fit

Model	df	AIC	ΔAIC
Baseline (BS and HO × herring abundance) + rate (BS and HO × herring abundance)	24	63,393.0	0
Baseline (BS and HO × herring abundance) + rate (BS and HO + herring abundance)	19	63,406.1	13.1
Baseline (BS and HO + herring abundance) + rate (BS and HO × herring abundance)	19	63,454.9	61.9
Baseline (BS and HO + herring abundance) + rate (BS and HO + herring abundance)	14	63,480.2	87.2
Baseline (BS and HO + herring abundance) + rate (BS and HO)	13	63,492.7	99.6
Baseline (BS and HO) + rate (BS and HO + herring abundance)	13	63,850.5	457.5
Baseline (BS and HO) + rate (BS and HO)	12	64,591.7	1,198.7

Note: df = degrees of freedom; ΔAIC = difference in AIC value with the best-supported model.

was abundant compared with when herring was rare (fig. 1*e*, 1*f*).

The probability density functions of mortality show that the probability of a hatchling to die at a certain age was always highest directly after hatching and confirm that early-life mortality was most sensitive to herring abundance (fig. 2). Among single and third-hatched chicks, herring abundance mostly affected mortality in the first week of life (fig. 2*a*, 2*f*), while for the other chicks this period was extended to varying degrees (fig. 2*b*–2*g*).

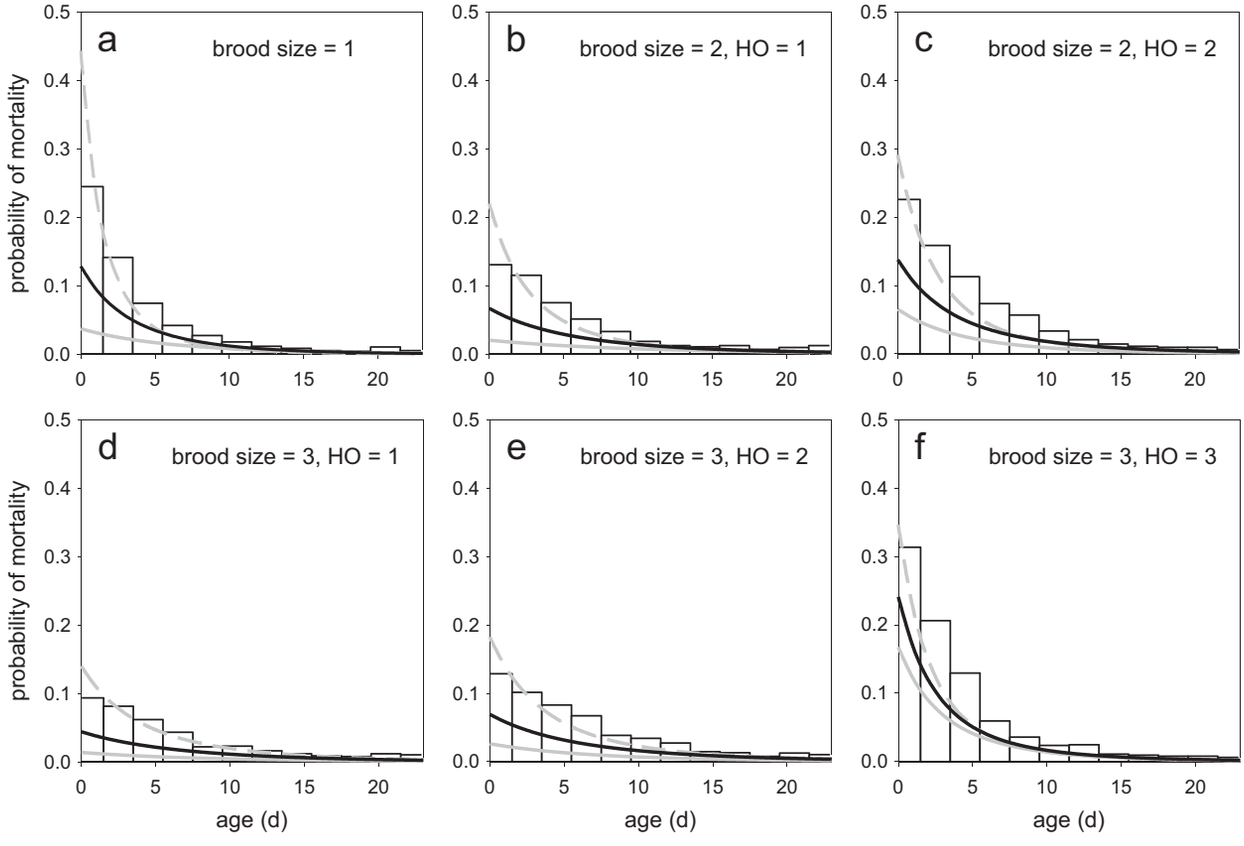
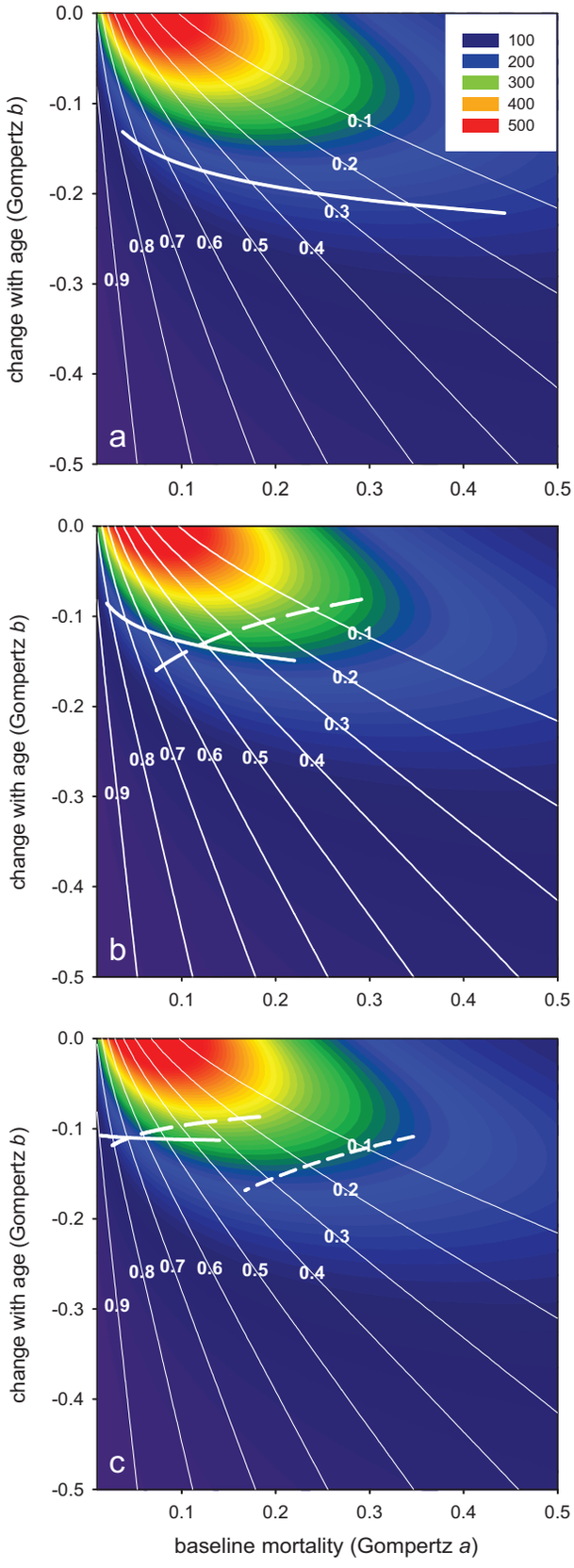


Figure 2: Gompertz mortality probability density functions of common tern chicks of all combinations of brood size and hatching order. Solid black lines represent the estimates for average herring abundance, solid gray lines represent the estimates for high herring abundance (+2 SD), and dashed gray lines represent the estimates for low herring abundance (−2 SD). Bars represent the overall proportion of hatchlings in that category that have died, regardless of herring abundance, subdivided over 2-day age categories. Note that more chicks hatched in years with below-average herring abundance.



Consequences for Energy Wasted on Nonfledged Chicks

Figure 3 shows how the fledging probability and the amount of metabolizable energy wasted (kJ) by it being consumed by the proportion of chicks that did not fledge per chick that hatched vary within a theoretical range of parameter space for Gompertz *a* and *b*. The solid lines in figure 3, which represent the actual parameter space observed for common tern chick mortality, show that despite fledging probability being strongly affected by herring abundance for chicks of all brood sizes and hatching orders, the parameter space of the Gompertz function that would in theory result in the largest waste of metabolizable energy per chick that hatches is never encountered. Yet the parameter space that would in theory minimize the waste on nonfledged chicks per chick that hatched is also not utilized.

In particular, for single chicks, the amount of energy wasted per chick that hatched is estimated to be low and to remain relatively stable with herring abundance (figs. 3*a*, 4*a*), despite the proportion of nonfledged chicks increasing with decreasing herring abundance (figs. 3*a*, 4*d*). This indicates that the energy wasted per chick that did not fledge decreases when herring becomes less abundant (fig. 4*g*). For first-hatched chicks in broods with siblings, the energy wasted per chick that hatched is estimated to decrease with increasing herring abundance (figs. 3*b*, 3*c*, 4*b*, 4*c*). However, this is only because the proportion of chicks that did not fledge decreases with increasing herring abundance (figs. 3*b*, 3*c*, 4*e*, 4*f*), because the amount of energy wasted per chick that did not fledge is estimated to increase when herring becomes more abundant (fig. 4*h*, 4*i*). In contrast, the amount of energy wasted per chick that did not fledge is estimated to be relatively unaffected by herring abundance for last-hatched chicks in broods with siblings and to always be smaller than that for earlier-hatched chicks (fig. 4*h*, 4*i*).

Discussion

We here suggested a parametric framework of how to interpret offspring preindependence age-specific mortality under varying environmental conditions. Since, from an evolution-

Figure 3: Contour plots of Gompertz parameter space with decreasing mortality hazard with age. Colors represent the estimated amount of metabolizable energy wasted (kJ) by being consumed by nonfledged chicks per chick that hatched under the specific Gompertz parameter combination. Isolines represent the fledging success (probability to reach the age of 24 days) for a chick that hatched under the specific Gompertz parameter combination. Actual Gompertz parameter combinations observed for common tern chick mortality in relation to food abundance (see lines in fig. 1) are represented by solid lines (from left [+2 SD of herring abundance] to right [−2 SD of herring abundance]) for single chicks (*a*), first-hatched (solid line) and second-hatched (long-dashed line) chicks in broods of two (*b*), and first-hatched (solid line), second-hatched (long-dashed line), and third-hatched (short-dashed line) chicks in broods of three (*c*).

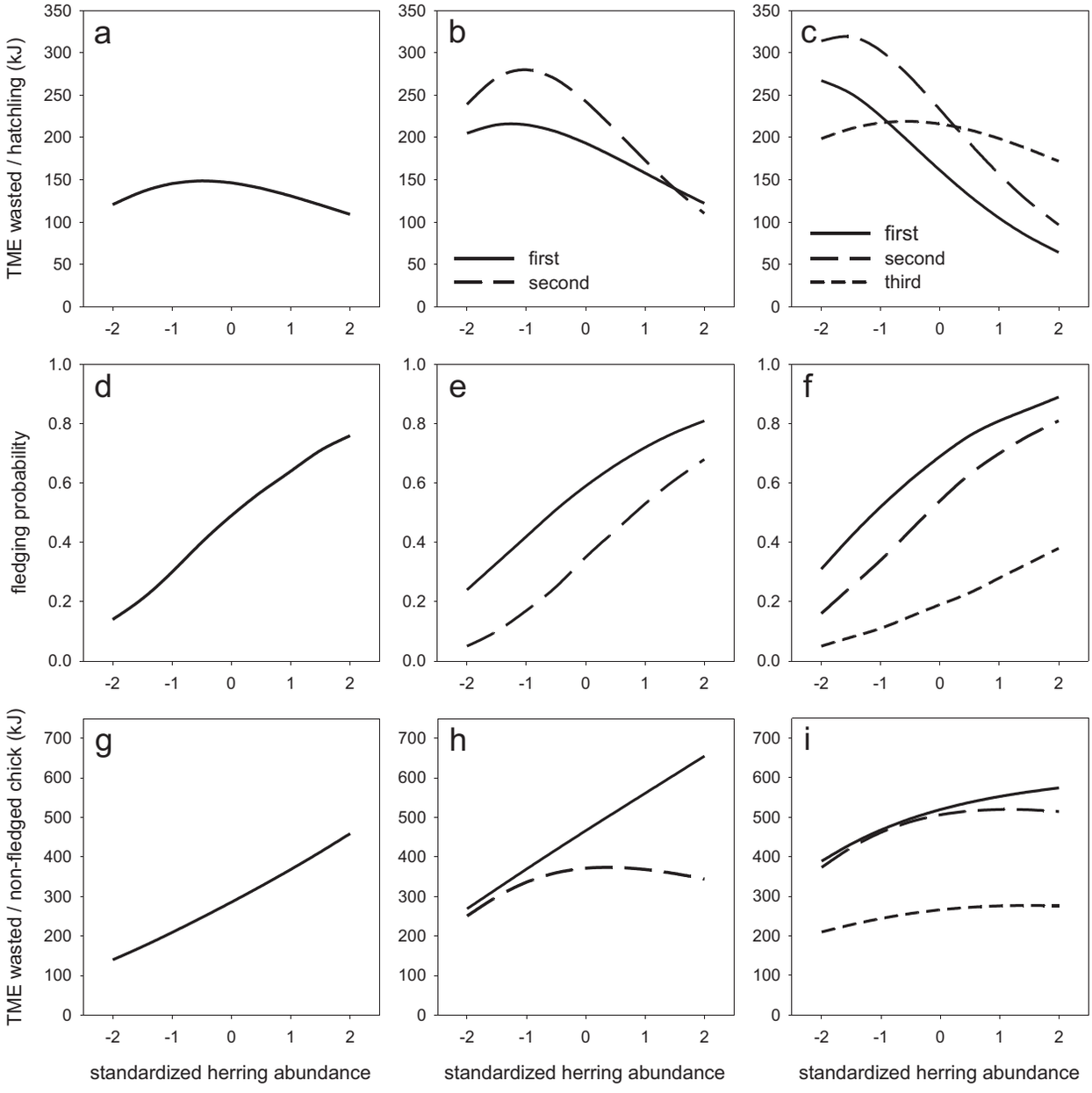


Figure 4: Estimated total metabolizable energy (TME) wasted on nonfledged chicks per chick that hatched (*a–c*), fledging success per chick that hatched (*d–f*), and TME wasted per chick that did not fledge (*g–i*), in relation to standardized herring abundance, for brood sizes 1–3, respectively.

ary perspective, such mortality cannot be interpreted without considering its effect on kin (Hamilton 1966), we estimated the amount of energy consumed by offspring that never reached independence—and therefore did not positively contribute to fitness—as a proxy for their cost to parents and/or siblings.

We found baseline mortality to be high and to increase with decreasing herring abundance. Although it is typical for mortality to peak at the start of life, early offspring mortality is often interpreted to be due to constraints rather than adaptation (Levitis 2011). It is inevitable that young individuals are smaller than adults, and small size may cause individuals to be more susceptible to predation or stochastic events, such as bad weather. However, in the case of common terns and many other birds, small chicks are more easily covered and brooded by the parents, and their energy requirements are rel-

atively small. Hence, early-life characteristics that may be considered constraints on survival from the offspring's perspective may not necessarily be insurmountable with additional parental allocation to reproduction. This makes it very difficult to empirically separate offspring constraint from adaptive parental restraint. Alternatively, individual offspring may vary in age-independent mortality hazard (frailty) from the onset of life, causing an increase in survival with age to be due to selective disappearance of more frail individuals rather than a within-individual decrease of mortality hazard with age (Vaupel and Yashin 1985). But why would such between-individual variation in frailty be maintained in the population? Only when the strength of selection against the traits underlying frailty would be weak could variation be maintained (Waddington 1942; Stearns and Kawecki 1994). As such, this argument is not independent from that considering the strength of selection against mortality to increase with age because of a later age of mortality wasting more resources that could otherwise have been utilized by kin (Hamilton 1966; Lee 2003, 2008). Indeed, we show that the variation in mortality hazard that is explained by annual variation in herring abundance was high directly after hatching but declined rapidly with age. Rather than interpreting this variation as resulting solely from weak selection against mortality at an early age, we suggest that the specific response of age-specific offspring mortality to food abundance may be shaped by benefits to parents.

Despite egg production and incubation being costly (Monaghan et al. 1998; Ruiz et al. 2000; de Heij et al. 2006), parents may benefit from producing an optimistic clutch size if food availability varies unpredictably, with offspring numbers being rapidly reduced when food turns out short (Temme and Charnov 1987; Kozlowski and Stearns 1989). Our framework shows that reducing offspring numbers along the axis of the baseline mortality (Gompertz *a*) rather than along the axis of the rate of change in mortality with age (Gompertz *b*) is far less costly in terms of energy wasted on nonfledged chicks (fig. 3). As such, the lower sensitivity of the rate of change in chick mortality with age to herring abundance can be explained by brood reduction in response to food shortage being more cheaply achieved by varying baseline mortality rather than the rate of change in mortality with age to food availability.

As originally proposed by Lack (1947), hatching asynchrony, together with other supporting maternal effects (e.g., egg size: Slagsvold et al. 1984; prenatal androgen deposition: Muller and Groothuis 2013), may aid cheap adjustment of brood size to unpredictable food conditions by establishing a clear hierarchy among siblings that is rapidly lethal to the last-hatched offspring when food is limited. In support of this prediction, we found that last-hatched chicks died earlier and more frequently than their older siblings and that the amount of energy wasted per nonfledged last hatchling was lower and less sensitive to herring abundance than that wasted on earlier-hatched nonfledged chicks. Hence, last hatchlings may indeed be primed for a rapid and cheap death when food availability is insufficient for the entire brood. This may come at a cost to their survival in good years, as in particular third-hatched chicks also did not achieve high fledging success in years with high herring abundance.

Although the observed combination of baseline and age-specific mortality was generally not within the most expensive parameter space of the Gompertz mortality function, the parameter space that would result in the cheapest production of an initial excess number of offspring also was not utilized (fig. 3). A further increased sensitivity of baseline mortality to food availability can perhaps be physiologically achieved only by producing hatchlings with energy reserves or competitive ability so small that their survival would also be compromised under good conditions. Similarly, a faster improvement of survival with age may be difficult to achieve physiologically. Alternatively, sibling competition—with each chick aiming to maximize its own survival at the expense of siblings—may cause suboptimal patterns of brood reduction from the parents' perspective, creating parent-offspring conflict (Godfray and Parker 1991; Muller et al. 2007; Vedder et al. 2017). The latter is supported by our estimate of energy wasted on nonfledged chicks per hatchling produced to be the lowest for chicks without siblings because of their baseline mortality being most sensitive to food abundance. When competition between siblings cannot interfere with the transfer of food from parents to specific offspring, parents may be better able to adjust offspring number to food availability in their own best interest. Hence, even though competition between siblings with different starting positions may aid in brood reduction, brood reduction may be most efficient when there is no possibility of competition. However, we cannot exclude the possibility that parents that hatch only one chick represent a nonrandom group that is somehow more economic in adjusting early offspring mortality to food availability. Young and inexperienced adult common terns typically have smaller broods (Zhang et al. 2015). Despite their small brood size, they may be disproportionally constrained—or restrained—in provisioning their offspring when food is short, causing earlier chick mortality.

In general, the novel framework that we here provide illustrates that the sensitivity of age-specific offspring mortality patterns to environmental conditions will have consequences for the amount of energy wasted on unsuccessful offspring. As such, the way age-specific offspring mortality is dependent on the environment will be under natural selection, but predictive theory on the optimal response to selection would need to incorporate conflicting selection pressures between parents and offspring and between siblings with different starting positions. The results for common terns show that the way age-specific chick mortality de-

pended on herring abundance caused the energy wasted on unsuccessful offspring to be much less than inversely proportional to chick fledging success and may thus serve an adaptive function.

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Left, week-old common tern chick receiving a herring from its parent. After the first week, their survival probability increases considerably. *Right*, three recently hatched common tern siblings in a nest. The last-hatched chick is typically the first to die when food is short. Photo credit: Sandra Bouwhuis.